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LETTER

Latitudinal patterns of terrestrial phosphorus limitation over the globe

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Abstract

Phosphorus limitation on terrestrial plant growth is being incorporated into Earth system models. The global pattern of terrestrial phosphorus limitation, however, remains unstudied. Here, we examined the global-scale latitudinal pattern of terrestrial phosphorus limitation by analysing a total of 1068 observations of aboveground plant production response to phosphorus additions at 351 forest, grassland or tundra sites that are distributed globally. The observed phosphorus-addition effect varied greatly (either positive or negative), depending significantly upon fertilisation regime and production measure, but did not change significantly with latitude. In contrast, phosphorus-addition effect standardised by fertilisation regime and production measure was consistently positive and decreased significantly with latitude. Latitudinal gradient in the standardised phosphorus-addition effect was explained by several mechanisms involving substrate age, climate, vegetation type, edaphic properties and biochemical machinery. This study suggests that latitudinal pattern of terrestrial phosphorus limitation is jointly shaped by macro-scale driving forces and the fundamental structure of life.

KEYWORDS
Aboveground production, climate, fertilization regime, latitudinal gradient, phosphorus limitation

INTRODUCTION

Phosphorus (P) is one of the two major limiting nutrients (the other is nitrogen (N)) for terrestrial plant production (Cleveland et al., 2011; Elser et al., 2007; Vitousek et al., 2010). Phosphorus limitation on terrestrial plant production is traditionally viewed as important, but mainly in lowland tropical regions where soils are generally strongly weathered (Reich & Oleksyn, 2004; Vitousek, 1984; Walker & Syers, 1976). While increasing global syntheses suggest a more wide distribution of terrestrial P limitation on land than previously thought

(Augusto et al., 2017; Du et al., 2020; Elser et al., 2007; Hou et al., 2020), the global pattern and magnitude of terrestrial P limitation remain inadequately understood (Fleischer et al., 2019; Turner et al., 2018; Wang et al., 2020). An improved understanding of terrestrial P limitation at the global scale is required for accurately projecting P limitation on future carbon sequestration in terrestrial ecosystems (Du et al., 2020; Fleischer et al., 2019; Hou et al., 2020; Reed et al., 2015; Wieder et al., 2015).

A number of studies have explored regional and global patterns of P limitation in terrestrial ecosystems over the last four decades (Aerts & Chapin, 2000; Augusto et al., 2017; Du et al., 2020; Elser et al., 2007; Fay et al., 2015; Hou et al., 2020; McGroddy et al., 2004; Reich & Oleksyn, 2004; Vitousek, 1984; Vitousek et al., 2010; Yuan & Chen, 2009; Yuan et al., 2011). In general, a decline in the magnitude of P limitation with latitude has been suggested by studies that show a decrease in the N:P ratio of plant tissues (e.g. leaf, root and litter) or an increase in plant P concentration with latitude (Augusto et al., 2017; McGroddy et al., 2004; Reich & Oleksyn, 2004; Vitousek, 1984; Yuan & Chen, 2009; Yuan et al., 2011). However, a lack of significant change or a significant but weak decline in the magnitude of P limitation with latitude has been reported in several syntheses of terrestrial P-addition experiments (Augusto et al., 2017; Elser et al., 2007; Hou et al., 2020; Yue et al., 2017). The inconsistent results are perhaps due to methodological differences between the two kinds of studies (Chapin et al., 1986; Du et al., 2020; Güsewell, 2004).

Nutrient-addition experiments are considered the most direct way to study nutrient limitation (Borer et al., 2017; Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011), because such experiments, if designed well, can directly determine both the type and the magnitude of nutrient limitation at a site (Chapin et al., 1986). In addition, the data may be compared across sites if the experiments are designed with comparison in mind (Borer et al., 2017; Fay et al., 2015). However, currently available nutrient-addition experiments differ greatly in the fertilisation regimes (i.e. the type and quantity of fertiliser and experimental duration) and production measures (e.g. aboveground biomass production vs. stem volume increment) used (Hou et al., 2020). These differences make it a challenge to compare the magnitude, and even the type, of nutrient limitation across sites (Du et al., 2020; Elser et al., 2007; Harpole et al., 2011; Hou et al., 2020). Even with the same fertilisation regime and production measure across experiments (Borer et al., 2017; Fay et al., 2015), comparing nutrient-addition effect across natural terrestrial ecosystems could be difficult, because of varied soil sorption, microbial competition and loss (via leaching, runoff or erosion) of added nutrients, plant adaption to low fertility soils, plant age and community composition, etc., across sites (Čapek et al., 2018; Chapin et al., 1986). While leaf nutrient measures (e.g. leaf N:P ratio) can be easily determined and compared across sites, their uses to indicate nutrient limitaton may result in large uncertainties (Du et al., 2020; Güsewell, 2004; Townsend et al., 2007; Yan et al., 2017). This is because leaf nutrient measures can not only be determined by soil nutrient supply and plant nutrient demand, but also be affected by other factors (e.g. plant physiology and life history) (Güsewell, 2004; Reich & Oleksyn, 2004; Townsend et al., 2007).

Despite methodological challenges to ascertain the latitudinal pattern of terrestrial P limitation, a latitudinal decline in terrestrial P limitation has been expected for several reasons which are not exclusive (McGroddy et al., 2004; Reich & Oleksyn, 2004; Vitousek, 1984). It has been predicted by the substrate-age hypothesis, which states that geological disturbances such as glaciation have led, on average, to older and lower fertility soils at low latitudes than at higher latitudes (Reich & Oleksyn, 2004; Vitousek et al., 2010; Walker & Syers, 1976; Yang & Post, 2011). It can also be predicted from latitudinal decreases in mean annual temperature (MAT) and precipitation (MAP). High MAT and MAP may enhance P limitation directly by alleviating climate constrain on primary production and allowing primary production to be more responsive to other resources (e.g. P) (known as the synergistic effect) (Ladwig et al., 2012; Reich et al., 2020). They may also enhance P limitation indirectly through promoting plant growth and P demand (Michaletz et al., 2018; Sun et al., 2017) and reducing soil P supply either through leaching, runoff or erosion or via altering edaphic properties (e.g. soil particle size and pH) (Augusto et al., 2017; Hou et al., 2018), which we label the climate-demand/supply hypothesis. Moreover, MAT and MAP may affect P limitation via shaping vegetation type (the climate–vegetation-type hypothesis). For example, with increasing MAP, vegetation type shifts from grassland vegetation to forest, the latter of which has been found to be more P-limited than the former (Elser et al., 2007; Hou et al., 2020), probably because of generally higher P demand, lower soil P availability and more acidic soils in forests than in grasslands (Alt et al., 2011; Chen et al., 2003).

However, a latitudinal increase in P limitation may be observed, if the positive influences of temperature on P limitation described above are dominated over by temperature constrain on the mineralisation of soil organic P, movement of P in soil or uptake of P by root (the temperature–biogeochemistry hypothesis), or by high P demand to offset temperature constrain on plant biochemical reactions (the temperature–plant physiology hypothesis) (Reich & Oleksyn, 2004; Vitousek et al., 2010). Finally, a constant magnitude of P limitation along latitude may be observed, if terrestrial P limitation is determined mainly by the biochemical machinery shared by all autotrophs (the biochemical machinery hypothesis) (Elser et al., 2007; Loladze & Elser, 2011; Sterner & Elser, 2002).

Our previous study revealed a significant decrease in the magnitude of P-addition effect with latitude in wetlands and croplands but not in forests, grasslands or tundra (Hou et al., 2020). Here, we further explore why we did not find the expected latitudinal decline in P-addition effect in forests, grasslands and tundra, which together occupy about three-quarters of the global vegetated land area (European Commission Joint Research Centre, 2003). We hypothesised that the spatial pattern of the observed P-addition effect, as well as the impact of climate and ecosystem properties on that effect size, was masked by the differences in fertilisation regimes and production measure among experiments (the methodology hypothesis). Once fertilisation regime and production measure are standardised, P-addition effect will decrease with latitude, which may be mediated by MAT and MAP and ecosystem properties such as vegetation type, soil P availability and soil particle size.

MATERIALS AND METHODS

Overview

The dataset used in this study is an extension of our previously published dataset in the forests, grasslands and tundra (Hou et al., 2019, 2020). Our previous dataset included only the latest measurement of plant response to the highest level of P addition in each experiment to avoid pseudoreplication in studying the global distribution and magnitude of P limitation (Hou et al., 2020). In this study, we extended the dataset by including time series of plant response to all levels of P addition in each experiment to explore how experimental duration and P-addition quantity would affect P-addition effect both at individual sites and across sites. We used the study site as a clustering variable in our statistical analyses to account for the dependence among multiple observations of plant response to P additions at a site. Observations of community-level leaf P and N concentrations and N:P mass ratio were collected and added to the new dataset to explore the consistency between them and P-addition experiments in indicating latitudinal gradient in P limitation. Data collection, preparation and analyses are described briefly as follows, with more details in Text S1. Additional details regarding data collection and preparation can also be found in Hou et al., (2020).

Data collection, description and preparation

In total, we collected 1068 observations of plant response to P addition from 351 experiments reported in 172 published papers, including 134 experiments in forests, 203 experiments in grasslands and 14 experiments in tundra (Fig. S1). While the type of P fertiliser may affect P-addition effect, most studies used only one type of P fertiliser. Therefore, when multiple forms of P fertilisers were tested, we chose the treatment of single superphosphate or triple superphosphate, if available. Although aboveground biomass production may be the best measure of aboveground primary production, we also accepted proxy variables that are known to be correlated with aboveground biomass production. For each observation of production, besides the mean value, the standard deviation and sample size were also recorded to calculate the weight of each observation used in statistical analyses. Moreover, we recorded a variety of site information as summarised in Table S1 and Fig. S2. Based on the statistical summary of fertilisation regimes (Fig. S2), we excluded observations with P-addition quantity >700 kg ha^{-1} or experimental duration >20 years from the following statistical analyses to avoid the influences of outliers on our results. Soil total P and organic C concentrations were $\log_{10}$ transformed to ensure normality before statistical analyses.

The response of aboveground primary production to P additions (i.e. P-addition effect) can be defined either in a relative way (i.e. response ratio or proportion) or in an absolute way (i.e. production change, unit: Mg dry biomass ha^{-1} $year^{-1}$). We calculated P-addition effect in both ways and performed statstical analyses on both measures of P-addition effect. However, we mainly showed results on the relative P-addition effect, because the absolute effect can be calculated only in 25 of the 134 forest experiments. Unless noted, we expressed P-addition effect in the relative way, which was natural log transformed for all statistical analyses but was back-transformed to percentage change to facilitate interpretations.

Exploratory analyses

We explored bivariate relationships between the observed P-addition effect and site properties using meta-analysis via a multilevel linear model with study site as the clustering variable in the "*metafor*" package version 2.4.0 (Viechtbauer, 2010) in *R* version 4.0.2 (R Core Team, 2020). All the bivariate relationships except those in tundra (due to a small sample size) were fitted with either a linear or quadratic regression. If the corrected Akaike's Information Criterion (*AICc*) value of a quadratic regression was 2 units less than that of a linear regression, the quadratic regression would be selected as the final model (Burnham & Anderson, 2002); otherwise, the linear regression was selected.

The main purpose of our statistical analyses is to adjust the observed P-addition effect according to a standardised fertilisation regime and a standardised measure of aboveground primary production. We first standardised P-addition effect by fertilisation regime and production measure using a division (for numerical variables) or mean adjustment (for categorical variables) method or using a regression residual method, as described in detail in Text S1. These simple methods did not work well (Tables S2 and S3), perhaps due to not accounting for the complicated interactions of fertilisation regime, production measure and site properties on P-addition effect (Table S4). We, therefore, used a more comprehensive method (i.e. MetaForest analysis) to standardise P-addition effect.

MetaForest analyses

MetaForest analysis is a recently developed method that can be used to explore heterogeneity in meta-analysis using random forests (Van Lissa, 2017, 2020). It has several advantages over traditional meta-analysis and regression analyses. The advantages include a high explantory power and abilities to consider unequal weights among experiments, many moderators, complicated interactions among moderators and nonlinear relationships between moderators and the predicted variable. In brief, we constructed MetaForest models to predict P-addition effect under a standardised fertilisation regime (i.e. 100 kg P ha^{-1} during 3 years in the form of triple superphosphate) and a standardised production measure (i.e. aboveground biomass production). By linking the predicted and the observed P-addition effects to latitude and site properties, we can test the methodology hypothesis.

We constructed MetaForest models separately for forests and grasslands (including tundra sites). We used study site as a clustering variable and as many moderators as possible in our original models (14 in forests and 13 in grasslands) to well account for the variation in the observed P-addition effect. For both the forest and the grassland models, the moderators included fertilisation regimes (including experimental duration, P-addition quantity and P fertiliser type), production measure, climate (including MAT and MAP), soil type, soil total P and organic C concentrations, soil sand content, soil pH and parent material type. Moreover, the forest model included forest age and forest type as the moderators; the grassland model included ecosystem type (grassland vs. tundra) as the moderator.

MetaForest models require complete moderator values for predictions. We filled missing values of MAT (validation $R^2 = 0.89$), MAP (validation $R^2 = 0.55$) and soil type (38% accuracy) with values derived from global maps (Fig. S3a–c; Table S5). Missing values of soil total P and organic C concentrations, sand content and pH cannot be appropriately derived from global maps (validation $R^2 = 0.01–0.36$; Fig. S3d–g; Table S5), and were, therefore, filled using the multivariate imputation by the chained equations with random forests method (out-of-bag $R^2 = 0.57–0.74$; Fig. S4) in the '*miceranger*' package version 1.3.5 in *R* (Wilson, 2020).

We performed MetaForest analyses generally according to Van Lissa (2020) using the *R* package "*metaforest*" version 0.1.3 (Van Lissa, 2017). In brief, we first checked the convergence of our original model, then pre-selected moderators, tuned model parameters, selected the final model and finally checked the convergence of the final model. Our original model included all moderators. To avoid model overfit, we pre-selected moderators using a recursive algorithm, which was replicated 100-fold. We used the R package *caret* version 6.0–86 (Kuhn, 2008) to tune model parameters, which included the number of candidate moderators at each split, and a minimum node site. We selected the model with the smallest root mean square error (RMSE) among all candidate models as our final model based on five-fold clustered cross-validation. We evaluated model performance by looking at the retrodictive R^2, RMSE and the predictive R^2 values: R^2 obtained during cross-validation (R^2_{cv}) and R^2 obtained during out-of-bag tests (R^2_{oob}) (Van Lissa, 2020). We used the final models for predicting P-addition effect under the standardised fertilisation regime and production measure (hereafter *the standardised P-addition effect*). We repeated MetaForest analyses five times and used the averages. After standardised with fertilisation regime and production measure, multiple values of P-addition effect at a site are theoretically the same and thus were averaged for further statistical analyses.

The standardised P-addition effects in relations to latitude and site properties

Similar to the observed P-addition effect, relationships between the standardised one and site properties were fitted with either a linear or a quadratic model based on the *AICc* criterion. We performed structural equation modelling (SEM) analysis on data across ecosystem types to test the climate–vegetation hypothesis and on data within ecosystem types to test the climate-demand/supply hypothesis. All SEM analyses were performed using the *R* package "*lavaan*" version 0.6–7 (Rosseel 2012).

RESULTS

Fertilisation regime and production measure and their influences on the observed P-addition effect

Fertilisation regime and production measure varied among observations of P-addition effect and ecosystem types as well as along the latitudinal gradient (Figure 1 and S2). P-addition quantity was significantly ($p < 0.05$, as follows) lower in forests (mean 139 kg P ha^{-1}) than in grasslands (220 kg P ha^{-1}), while the opposite was true for experimental duration (4.6 years in forests and 3.4 years in grasslands) (Figure 1 and S2). P-addition quantity tended ($p = 0.05$) to be lower at the inner tropical regions (0–15 °N/S; 119 kg P ha^{-1}) than at other latitudes (193 kg

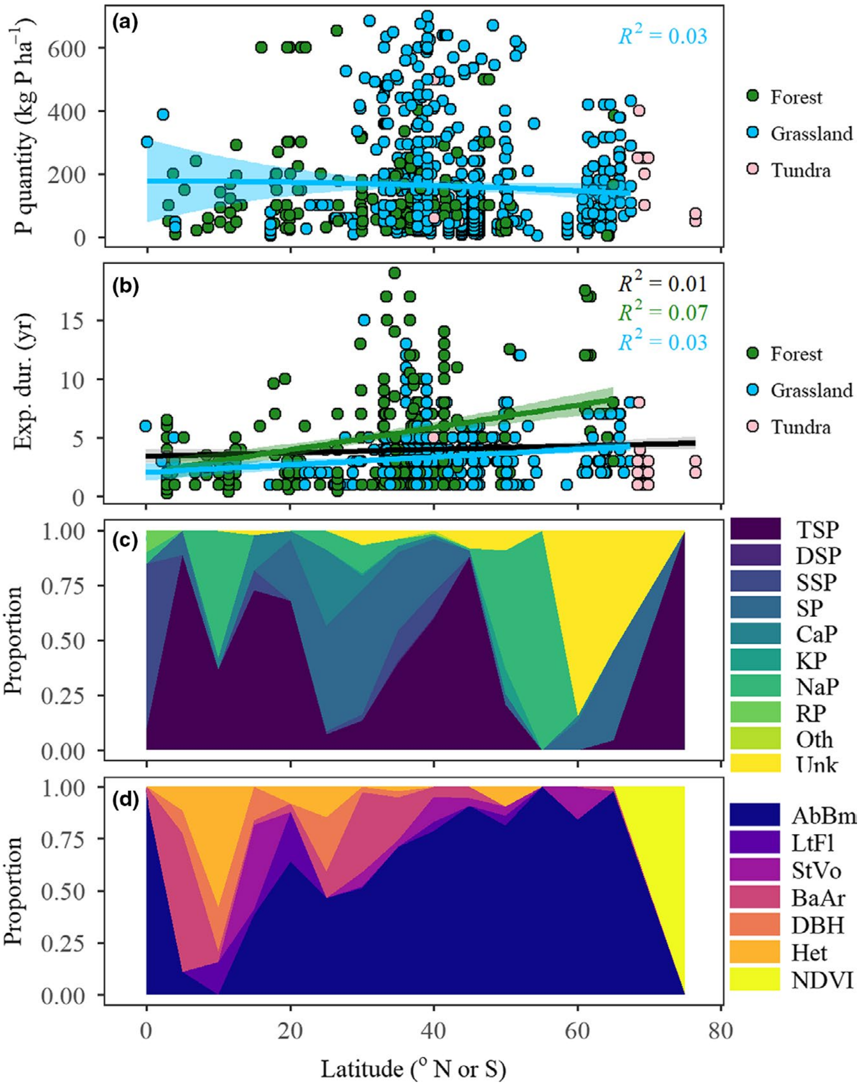

FIGURE 1 Fertilisation regime and production measure varied with latitude. (a) P-addition quantity. (b) Experimental duration. (c) P fertiliser type. (d) Production measure. P fertiliser type and production measure are binned by every five absolute latitudinal degrees (e.g. 0°–5° N/S). Statistical analysis is performed in forests (green), grasslands (blue) or across ecosystem types (black). If one relationship is statistically significant ($p < 0.05$), a regression line, 95% confidence interval (shaded area) and R^2 are shown. P fertiliser types include triple superphosphate (TSP), double superphosphate (DSP), single superphosphate (SSP), calcium phosphate (CaP), potassium phosphate (KP), sodium phosphate (NaP), superphosphate (SP), others (Oth) and unknown (Unk). Production measures include the production of aboveground biomass (AbBm) or litterfall (LtFl) and the increase rate of stem volume (StVo), basal area (BaAr), diameter at breast height increment (DBH), height (Het) or normalised difference vegetation index (NDVI)

P ha^{-1}) (Figure 1a). Experimental duration increased significantly with latitude both within and across ecosystem types (Figure 1b). Both P fertiliser type and production measure type also varied with latitude (Figure 1c and d). Moreover, site properties such as climate and soil total P concentration varied with latitude (Fig. S5) as well as among ecosystem types (Table S1).

Experimental duration, but not P-addition quantity, positively affected the observed P-addition effect, both within and across ecosystem types (Figure 2a and b). Both experimental duration and P-addition quantity also positively affected the observed P-addition effect in some individual experiments with multiple levels of P addition and/or multiple times of observations (Figs S6 and S7). P fertiliser types and production measures significantly influenced the observed P-addition effect in forests as well as across ecosystem types (Figure 2c and d). Moreover, fertilisation regime interacted with site properties (e.g. MAT and soil total P concentration) on the observed P-addition effect (Table S4).

The observed versus the standardised P-addition effects

Our MetaForest models explained 95% and 90% of the variation in the observed P-addition effect in forests and grasslands, respectively (Table S6), with fertilisation

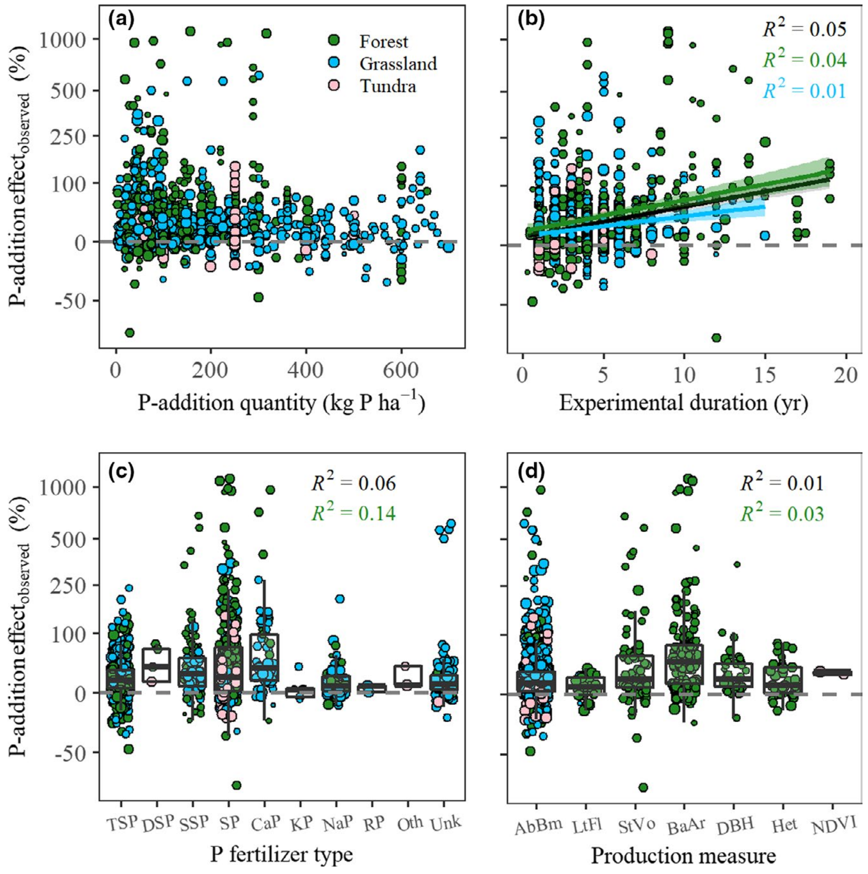

FIGURE 2 Observed P-addition effect in relation to fertilisation regime and production measure. Observed P-addition effect versus (a) P-addition quantity, (b) experimental duration, (c) P fertiliser type and (d) production measure. Statistical analysis is performed in forests (green), grasslands (blue) or across ecosystem types (black). If one relationship is statistically significant ($p < 0.05$), a regression line (for numeric predictor only), 95% confidence interval (shaded area, for numeric predictor only) and R^2 are shown. Point sizes are proportional to weights used for statistical analyses. Dashed grey line separates P-addition effect from positive from negative values. In (c) and (d), the thick horizontal line represents the median of the distribution, the box includes 50% of the data and the whiskers reach the highest and lowest value within 95% of the distribution. Full names of P fertiliser type and production measure are the same as given in Figure 1

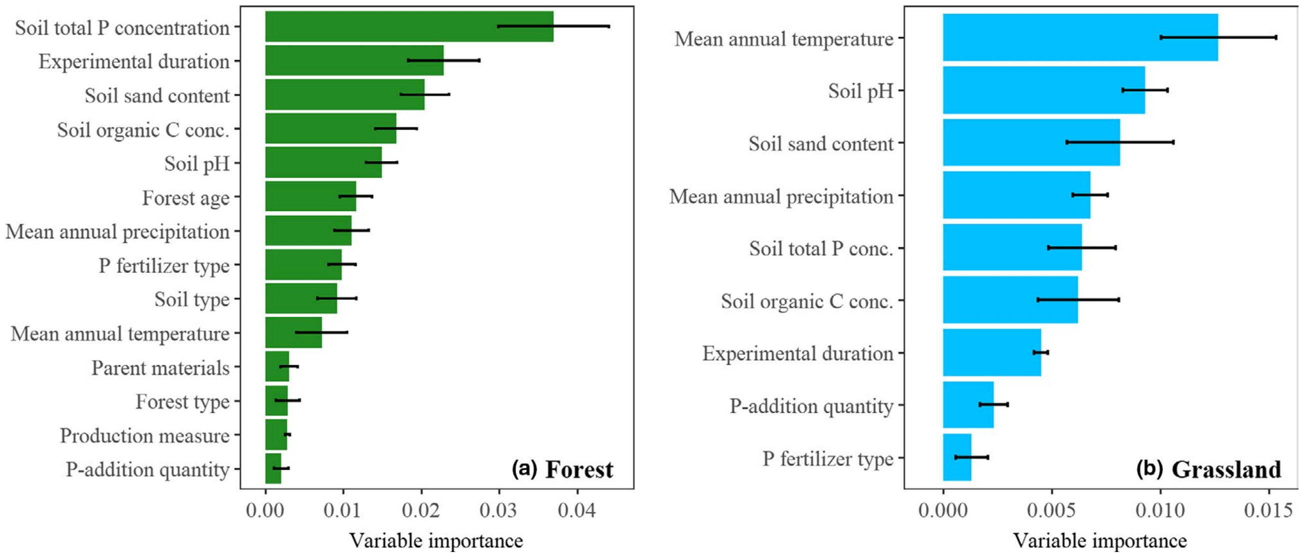

FIGURE 3 Relative importance of variables in predicting variation in the observed P-addition effect. (a) Forest; (b) Grassland. Relative importance is quantified using MetaForest analyses (see details in Text S1). Error bars indicate standard errors

regimes, climate and soil properties all as important moderators (Figure 3). Forest age and forest type were also important in explaining variation in the observed P-addition effect in forests (Figure 3a).

The observed P-addition effect did not change significantly with latitude either within or across ecosystem types (Figure 4a), which was consistent with previous syntheses of terrestrial P-addition experiments (Fig. S8). However, the standardised one decreased significantly with latitude across ecosystem types (Figure 4d). It decreased linearly with latitude in grasslands, yet showed a unimodal relationship with latitude in forests (Figure 4d). Different latitudinal patterns between the observed and the standardised P-addition effects were because of the standardisation of fertilisation regime and production measure as well as the removal of the unexplained variation in the observed P-addition effect (Fig. S9; Table S6).

While the observed P-addition effect was not related to MAT or MAP either within or across ecosystem types (Figure 4b and c), the standardised one increased linearly with MAT in the full dataset as well as in grasslands and varied unimodally with MAT in forests (Figure 4e and S10). The standardised P-addition effect varied unimodally with MAP across ecosystem types, decreased with MAP in forests and had a convex relationship with MAP in grasslands (Figure 4f). Both the standardised and the observed P-addition effects decreased with leaf P concentration and increased with leaf N:P ratio across

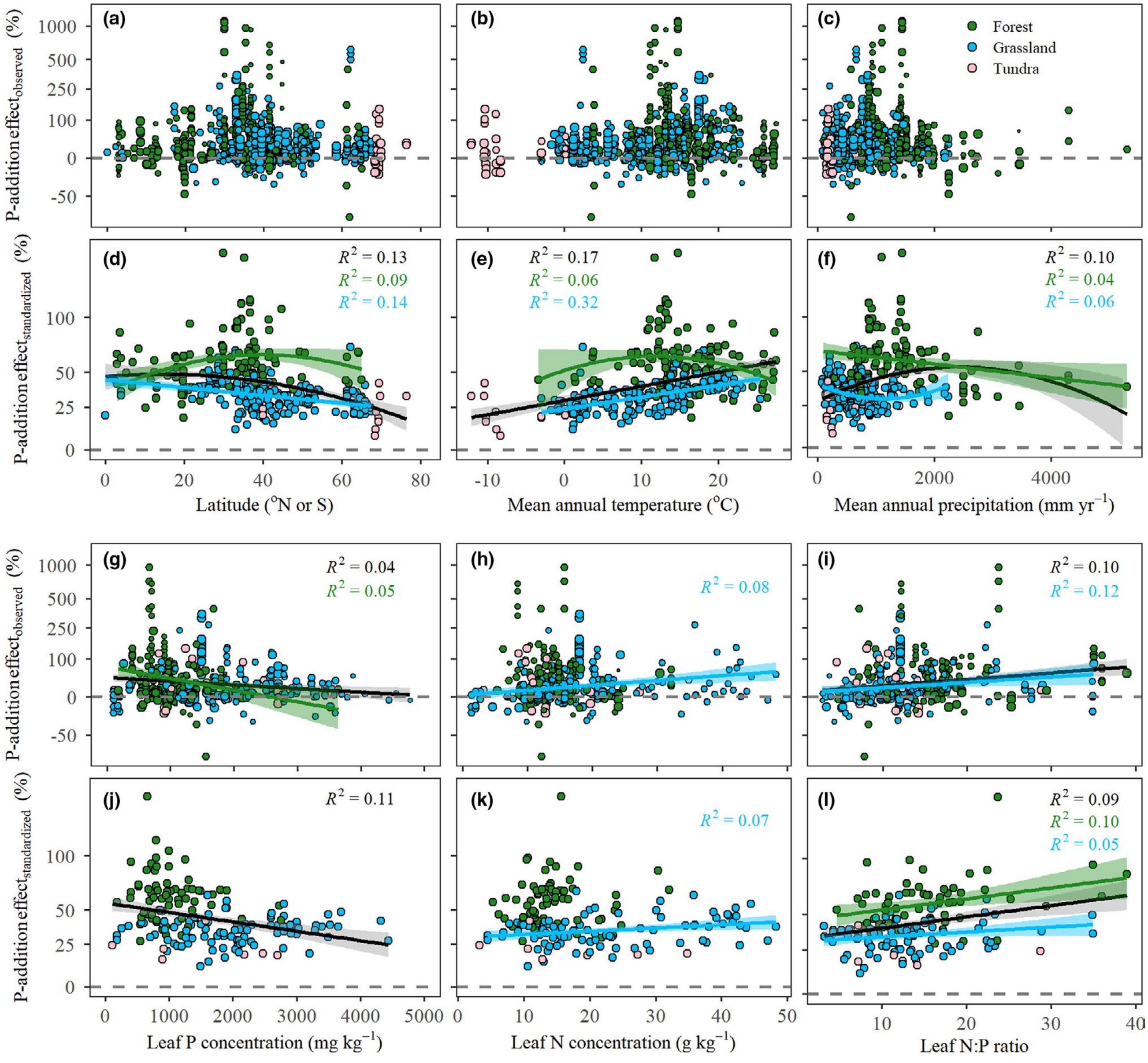

FIGURE 4 P-addition effect relates to latitude, climate and leaf nutrient measures. Statistical analysis is performed in forests (green), grasslands (blue) or across ecosystem types (black). If one relationship is statistically significant ($p < 0.05$), a regression line, 95% confidence interval (shaded area) and R^2 are shown. In (a)–(c) and (g)–(i), point sizes are proportional to weights used for meta-regression fits

ecosystem types (Figure 4). Like the relative P-addition effect, the absolute one showed generally stronger relationships with climate and leaf nutrients after standardisation with fertilisation regime and production measure (Fig. S11).

The observed P-addition effect was significantly higher in forests (33.9%), especially in needleleaf evergreen forests (50.4%), than in grasslands (22.6%), which all tended to be higher than in tundra (12.8%) (Table S7). It also decreased significantly with soil total P concentration across ecosystem types as well as in forests (Table S7). These differences or relationships became more apparent after P-addition effect was standardised with fertilisation regime and production measure (Figure 5a and f). The standardised P-addition effect increased with soil sand content and decreased with soil pH and organic C concentration across ecosystem types (Figure 5b–d). Moreover, it decreased with forest age and was generally higher in the strongly weathered soils than in the slightly/intermediately weathered soils under forests (Figure 5f and g).

SEM analysis showed that latitudinal gradient in the standardised P-addition effect was mediated by MAT, MAP and vegetation (Figure 6a). In forests, it was mediated by MAT, MAP and soil physiochemical properties as well as forest type (Figure 6b). In grasslands, it was mediated by MAT, soil sand content and soil total P concentration (Figure 6c).

DISCUSSION

As hypothesised, fertilisation regime and production measure varied across observations of plant response to P additions, and such variations masked relationships between P-addition effect and latitude and site properties. After fertilisation regime and production measure were standardised, P-addition effect was significantly related to latitude, climate and several other site properties. The latitudinal decline in the standardised P-addition effect was generally consistent with what has previously been indicated by plant N:P ratio and P concentration or soil P supply (Aerts & Chapin, 2000; Augusto et al., 2017; McGroddy et al., 2004; Reich & Oleksyn, 2004; Yuan & Chen, 2009; Yuan et al., 2011). The standardised P-addition effect, as well as the observed one, increased with leaf N:P concentration and decreased with leaf P concentration, as predicted by the theory of ecological stoichiometry (Koerselman & Meuleman, 1996; Sterner & Elser, 2002). The questions remain open as to whether the latitudinal decline in the standardised P-addition effect involves direct or indirect effects of climate, changes

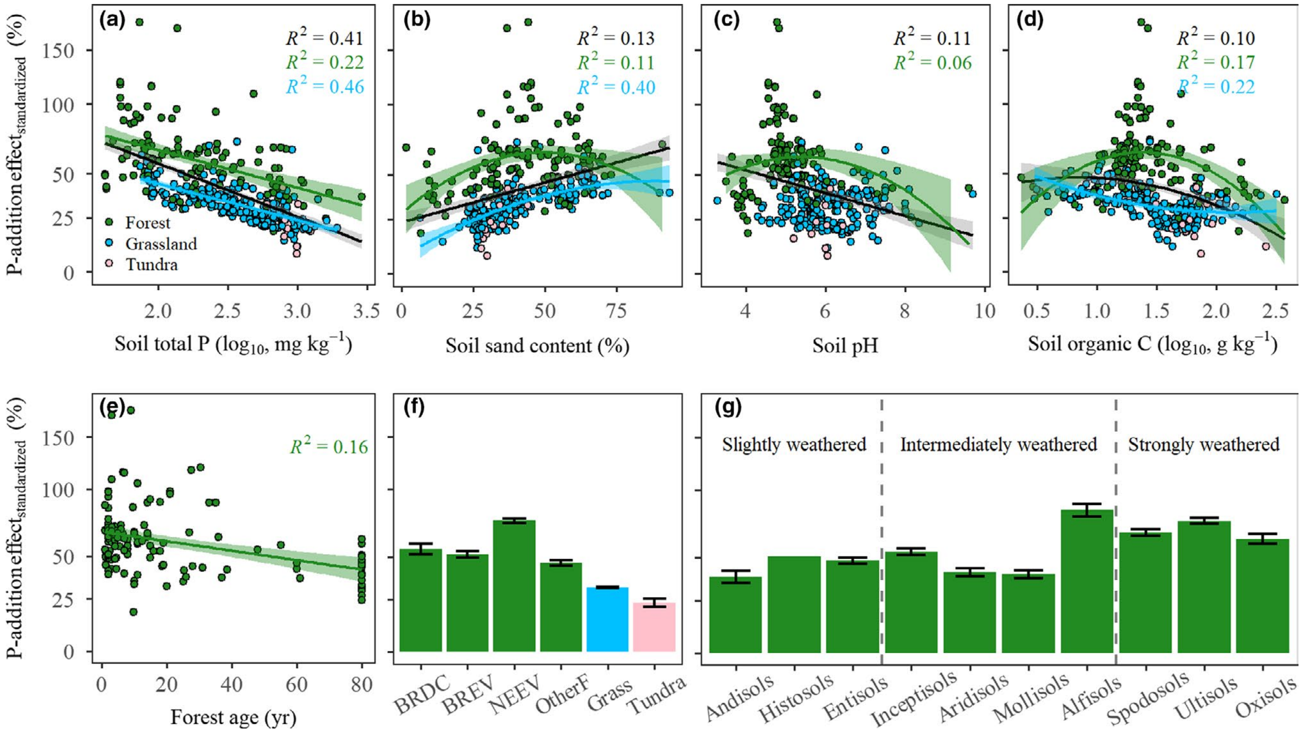

FIGURE 5 Standardised P-addition effect in relation to site properties. Site properties include soil (a) total P concentration, (b) sand content, (c) pH and (d) organic C concentration, (e) forest age, (f) vegetation type and (g) soil type. Statistical analysis is performed in forests (green), grasslands (blue) or across ecosystem types (black). If one relationship is statistically significant ($p < 0.05$), a regression line, 95% confidence interval (shaded area) and R^2 are shown. In (i), vegetation type included broadleaf deciduous forest (BRDC), broadleaf evergreen forest (BREV), needleleaf evergreen forest (NEEV), other types of forests (OtherF), grassland vegetation and tundra vegetation. In (f) and (g), error bars indicate standard errors

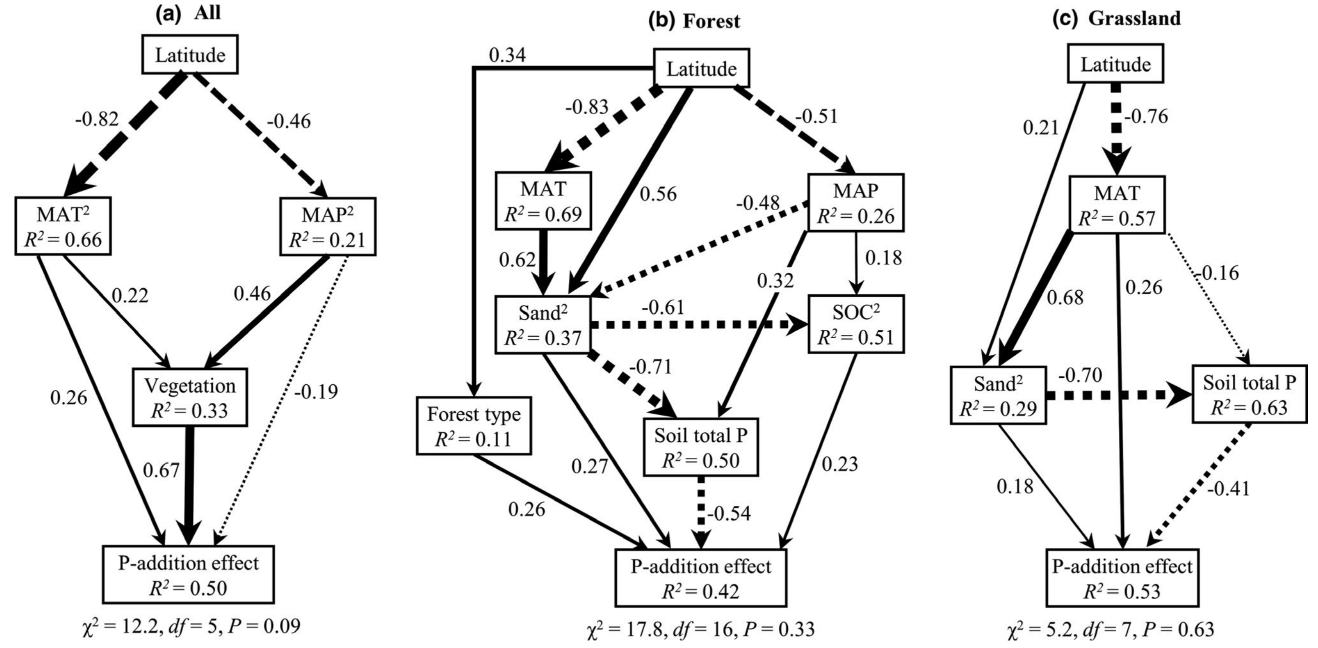

FIGURE 6 A structural equation model analysis of latitudinal gradient in the standardised P-addition effect. (a) Across ecosystem types; (b) forest; (c) grassland. Numbers on arrows are standardised path coefficients. Arrow width is proportional to the standardised coefficient. Continuous and dashed arrows indicate positive and negative relationships respectively. Variable with superscript 2 indicates the inclusion of quadratic term. Signs of pathways related to variables with a quadratic term indicate signs of pathways between the linear terms. Percentage near endogenous variable indicates the proportion of variance explained. In (a), signs of pathways related to the vegetation (categorical variable, i.e., forest vs. grassland) are not interpretable; thus, absolute values are presented. In (b), covariations among variables are not shown

in vegetation type, variability in soil P supply and physiochemical properties, substrate age or a combination thereof.

The latitudinal decline in the standardised P-addition effect is consistent with both the substrate-age and climate-demand/supply hypotheses and suggests that the magnitude of P limitation should generally increase with substrate age, MAT and MAP. An increase in the magnitude of P limitation with substrate age is also suggested by the generally larger standardised P-addition effects in the strongly weathered soils than in the lightly/moderately weathered soils (Figure 5g). A linear increase in the standardised P-addition effect with MAT and unimodal increase of it with MAP (Figure 4e and f) are also consistent with synergistic effect: less temperature constrain on primary production at high MAT and minimum precipitation constrain on primary production at moderate MAP (around 2500 mm year^{-1}) (Ladwig et al., 2012; Reich et al., 2020; Schuur, 2003).

Mediation of the latitudinal pattern of P-addition effect by vegetation type (Figure 6a) is consistent with the climate–vegetation-type hypothesis. Forests, shown to be more P-limited than grasslands (Figure 5f; Table S7), make up a greater fraction of all vegetation types in tropical regions than in temperate regions (Fig. S5k), thus contributing to the higher standardised P-addition effect in tropical regions. Stronger P limitation in forests than in grasslands was probably because of both higher P demand and lower soil P availability in forests (Table S1; Chen et al., 2003). Higher P demand in forests could be due to their higher primary productions (Gherardi & Sala, 2020; Sun et al., 2017) driven by higher MATs and MAPs than in grasslands (Huang et al., 2019; Knapp et al., 2017). Lower soil P availability in forests may be because of their larger P storages in plant biomass as well as more acidic soils than in grasslands (Table S1; Alt et al., 2011; Chen et al., 2003).

The consistently positive standardised P-addition effects along latitude confirms the worldwide distribution of P limitation on land (Augusto et al., 2017; Elser et al., 2007; Hou et al., 2020) and partly supports the biochemical machinery hypothesis (Elser et al., 2007; Sterner & Elser, 2002). This result suggests that the fundamental structure of life (i.e. chemical machinery) acts together with macro-scale driving forces (e.g. climate and substrate age) on the latitudinal pattern of terrestrial P limitation. However, there was no evident support for the temperature–biogeochemistry hypothesis or the temperature–plant physiology hypothesis. The lack of support may be because these influences were swamped in magnitude by the effects of substrate age, climate-driven demand/supply, vegetation type and the synergetic effects of climate and nutrients, or perhaps interactions with other processes (e.g. microbial immobilisation of P) limit the effects of these driving factors.

Latitudinal pattern of standardised P-addition effect varied among ecosystem types, with a linear decline in grasslands, yet a unimodal change in forests with increasing latitude, as mediated mainly by MAT. The dissimilar MAT impacts on the standardised P-addition effect between grasslands and forests were probably because of their different MAT optima of primary production (Duffy et al., 2021; Huang et al., 2019). Primary production typically increases with MAT up to an optimum MAT and decreases above the optimum MAT; the optimum MAT varies with vegetation type, and is generally lower in forests, particularly in needleleaf forests, than in grasslands (Duffy et al., 2021; Huang et al., 2019). Given the synergistic effects of climate and nutrients on primary production, MAT optima of P-addition effect may be similar to MAT optima of primary production, and thus may occur within our explored MAT range in the forests (mostly between 1°C and 27°C) but not in the grasslands (mostly between −2°C and 23°C) (Figure 4e).

The dissimilar MAT impacts on P-addition effect between forests and grasslands were probably also mediated by soil sand content (Figure 6). While MAT had a constant positive effect on soil sand content (Figure 6), soil sand content has dual effects on the response of primary production to P addition. On one hand, it facilitates the use of added P by plants due to its low P sorption capacity (Chapin et al., 1986; Maguire et al., 2001); on the other hand, it can lead to more loss of added P from soil via run-off and leaching (Chapin et al., 1986; Hou et al., 2018). In grasslands, where MAP is generally low, the positive influence of soil sand content on P-addition effect may overwhelm its negative influence, resulting in a net positive influence (Figure 5b). In forests, where MAP is generally high, soil P loss via run-off and leaching may not be significant at low soil sand contents but could be significant at high soil sand contents (Hou et al., 2018), resulting in a unimodal change in P-addition effect along soil sand content gradient (Figure 5b). MAP-driven loss of P from soil probably also explains the decline in the standardised P-addition effect with increasing MAP in the forests (Figure 4f). Finally, decrease in the standardised P-addition effect with MAT from 12.6 °C to 27.5 °C in the forests (Figure 4e) may be a consequence of the reduction in the fraction of needleleaf evergreen forest of all forest types (Fig. S10). The standardised P-addition effect was generally larger in needleleaf evergreen forests than in other types of forests (Figure 5f), probably because they are more responsive to P addition than other types of forests, or because needleleaf evergreen tree species are usually selected to cope with nutrient-poor soils during afforestation (Fig. S10; Corlett, 1999).

Community-level leaf N:P ratio has been used to indicate the type of nutrient limitation, that is, <14 or 10 indicates N limited, >16 or 20 indicates P limited and 14–16 or 10–20 indicates N/P co-limited (Güsewell, 2004; Koerselman & Meuleman, 1996). Both community-level leaf N:P ratio and P concentration have also been used to indicate differences in the magnitude of P limitation among sites in some previous studies (Aerts & Chapin, 2000; Hou et al., 2012). In our study, P-addition effect increased with leaf N:P ratio and decreased with leaf P concentration, which supports the idea of using community-level leaf N:P ratio and P concentration to indicate differences in the magnitude of P limitation among sites (Hou et al., 2012; McGroddy et al., 2004; Reich & Oleksyn, 2004). However, leaf N:P ratio <14 or 10 does not indicate P non-limitation; instead, it indicates a smaller magnitude of P limitation than leaf N:P ratio >14 or 10 (Figure 4i and l). Moreover, P-addition effect varied essentially at any given leaf N:P ratio or P concentration. This result was probably because leaf N:P ratio and P concentration not only reflect the magnitude of P limitation but also are affected by ecosystem properties such as plant physiology and nutrient use strategies (Güsewell, 2004; Townsend et al., 2008; Townsend et al., 2007). The result may also be because a given leaf N:P ratio could result from different combinations of leaf N and P concentrations (Güsewell, 2004).

Our results have important implications for understanding and modelling terrestrial P limitation. For example, the important influences of fertilisation regime on P-addition effect call for caution in comparing the magnitude of P limitation across experiments with different fertilisation regimes. The positive MAT impact on P-addition effect suggests that terrestrial P limitation may be enhanced due to future warming conditions. The consistently positive P-addition effect along latitude implies that Earth system models should consider P limitation on primary production not only in tropical regions but also in other regions (e.g. temperate regions).

Despite great efforts to compile data and standardise P-addition effects, our study has some limitations. First, boreal forests and tropical forests, especially those at mature stages, are largely underrepresented. More experiments from these ecosystems are needed to better represent global forest ecosystems. Second, key predictors of P-addition effect (e.g. soil total P concentration) are largely missing. The filled data could lead to considerable uncertainties in our standardised P-addition effects. Given these limitations, relationships revealed in this study may be regarded as working hypotheses from which to design targeted investigations that broaden the database and include more complete measurements of site properties. Third, variation in the observed P-addition effect was not fully accounted for by our MetaForest models before standardising P-addition effect. More advanced statistical methods may be developed in the future to standardise nutrient-addition effects across sites.

CONCLUSION

We standardised P-addition effect in a global database of P-addition experiments by fertilisation regime and production measure. We showed that the standardised P-addition effect was consistently positive and decreased significantly with latitude. The consistently positive P-addition effects may be explained by the biochemical machinery shared by all life on Earth. The latitudinal gradient was consistent with what has previously been indicated by latitudinal gradients in plant N:P ratio and P concentration and support hypotheses involving substrate-age, climate, vegetation type and edaphic properties. Our results suggest that the latitudinal pattern of terrestrial P limitation is shaped by both macro-scale driving forces and the biochemical machinery of life.

COMPETING FINANCIAL INTERESTS STATEMENT

The authors declare no conflict of interest.

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AUTHORSHIP

E.H. and Y.L. designed the study. E.H. collected the data. E.H. and Y.L. analysed the data. All authors contributed significantly to the writing of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and R scripts used in this study are deposited in Figshare (https://doi.org/10.6084/m9.figshare.14071301.v1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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